

NEST SITE CHARACTERISTICS OF AMERICAN ROBINS BREEDING IN DESERT-RIPARIAN HABITAT

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ABSTRACT.—We describe the nest site characteristics, and report on the association between site characteristics and reproductive success (brood size at day 8), for a population of American Robins (*Turdus migratorius*) breeding in the Toiyabe Mountains of central Nevada. Based on data from 132 nests, the immediate vicinity (a 10-m radius) around robin nests was sparsely vegetated with limited cover at any vegetation height. Nest tree diameters at breast height were not significantly different from those of nearby trees. Based on tree availability in the immediate vicinity, robins chose to nest in single-leaf pinyon (*Pinus monophylla*) more often (49.6% of nests used versus 39.3% availability), and quaking aspen (*Populus tremuloides*) less often (24.8% of nests used versus 52.1% availability), than expected by chance. Contrary to predictions based on previous studies, there was no change from coniferous to deciduous trees for nesting as the breeding season progressed, nor did robins build their nests higher in trees later in the season. Nest orientation was significantly directional in the 90° arc between east and south, but was unrelated to the amount of concealment conferred by shrub and bush cover in the four quadrants around the nest. Solar insolation resulting from nest placement was not related to brood size at day 8 and there were no discernable relationships between either solar insolation or orientation and clutch initiation date. Brood size on day 8 was inversely related to mean dbh of the surrounding trees, while canopy cover and height were associated positively with larger broods at day 8. Received 13 February 2002, accepted 20 February 2003.

Although researchers often know a great deal about the basic biology of endangered species, it is not unusual for similar information to be lacking for common species. The American Robin (*Turdus migratorius*) is a widespread North American species that is a habitat generalist, occupying residential areas, woodlands, open forests, as well as early through late seral forest, and showing broad acceptance of a variety of overstory species (Tyler 1949, Sallabanks and James 1999). Recent research has elucidated the diet, foraging ecology, and geographical variation in morphology and appearance of the robin (e.g., Wheelwright 1986, Aldrich and James 1991, Jung 1992, Sallabanks 1993). However, studies of this species' nesting habits and nest site characteristics have been limited, and often focused on human-altered landscapes such as agricultural settings, tree plantations, and ur-

ban areas (e.g., Howell 1942, Young 1955, Savard and Falls 1981, Yahner 1982, Hughes and Hudson 1997). Data on nest tree characteristics and nest placement presented in the review of the American Robin by Sallabanks and James (1999) were based on unpublished data with no comparisons made to the trees or placement opportunities that were available in the surrounding habitat.

Nest placement patterns, and any seasonal changes in those patterns, may be interpreted in the context of the relationship between selection of nest site characteristics and the risk of predation (e.g., Stauffer and Best 1986, Marzluff 1988, Möller 1988). For instance, American Robins exhibited seasonal changes in nest height (higher later in the breeding season; Howell 1942) and tree type selected for nest substrate (coniferous trees early in the season, deciduous trees later; Howell 1942, Savard and Falls 1981). These adjustments may be related to deterring predators in a changing environment. Likewise, Davidson and Knight (2001) suggested that within the relatively open landscape in which robins nest, placement of a nest in dense understory vegetation at a habitat edge might provide better cover than would interior forest locations. This presumed that nest depredation from visually oriented predators was an important selective factor. In the congeneric Eurasian

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Blackbird (*Turdus merula*), habitat structure was a significant predictor of nesting success during egg laying and incubation, when concealment may have prevented nest discovery, but not after eggs hatched and auditory cues became more important to predators (Hatchwell et al. 1996).

Our goal was to describe the nest site characteristics of American Robins breeding in a desert-riparian community. Our specific objectives were to (1) examine nest placement relative to the vegetation available immediately adjacent (within 10 m) to the nest, (2) look for changes in nest placement associated with seasonal changes in physiognomy, and (3) assess the potential association among local vegetation characteristics (microhabitat within 10 m of the nest), solar insolation, and the number of young present at day 8 of the nestling phase.

METHODS

We collected data during the summers of 1995–1996 in central Nevada. We searched for nests in canyons along five permanent streams (San Juan, Stewart, Clear, Marysville, and Washington Creek) on the western side of the Toiyabe Mountain Range (39° 30' N, 117° 05' W). Canyon floors typically are narrow with 4- to 50-m wide riparian zones dominated by stands of quaking aspen (*Populus tremuloides*) interspersed with willows (*Salix* spp.) and water birch (*Betula occidentalis*), along with grassy meadows densely populated by *Carex* spp., *Poa* spp., *Juncus* spp., and *Deschampsia* spp. (Weixelman et al. 1996). Canyon slopes adjacent to these riparian zones are steep, rocky and characterized by low density upland forests consisting largely of single-leaf pinyon (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*), and curl-leaf mountain mahogany (*Cercocarpus ledifolius*), with an understory of sagebrush (*Artemisia* spp.; Weixelman et al. 1996). These canyons were subject to varying levels of livestock grazing and use as recreational areas prior to and during the study, as well as natural disturbances, all of which altered the habitat to varying degrees (Weixelman et al. 1996).

We searched suitable habitat in all drainages beginning on 1 June 1995 and 1 May 1996 and continued until mid July of both years. During 1995, in addition to active nests

we also searched for previously constructed robin nests that had sufficient structure remaining to be positively identified. These additional nests are referred to hereafter as 1994 nests, although some may have been older and others may have been early 1995 nesting season failures. We monitored active nests every 3–4 days from discovery to the end of day 8 (first egg hatched on day 0) of the nestling phase, or until the nest failed. We determined the clutch initiation date, final clutch size, and number of young present at day 8 of the nestling phase for all nests. Day 8 was chosen for determining nesting success to avoid the potential premature fledging of young caused by such visits, and to limit the attraction of nest predators, particularly *Corvids*. Although most nest failures occur at the egg rather than nestling stage (Kendeigh 1942), as a consequence of our methodology we likely missed the loss to predators of some nestlings that occurred between day 8 and the normal date of fledging for this species on day 13 (Sallabanks and James 1999). Thus we may have overestimated the number of young produced from nests associated with certain characteristics. When we discovered nests after clutch completion or hatching, we estimated the age of the chicks based on an aging key we developed using the morphological characteristics of known-age chicks from seven nests (see Appendix). For these nests, we determined clutch initiation date based on a 13-day incubation period (Howell 1942, Young 1955). For any nests found after day 8, we assumed that the number of nestlings present on discovery had been present on day 8. Although we saw Brown-headed Cowbirds (*Molothrus ater*) on our study site, we found no evidence of cowbird parasitism in any robin nests. Our protocol did not allow us to distinguish between nest failures caused by adult abandonment due to predation, starvation, or cold weather and those due to predation of eggs or chicks. However, none of our data on chick mass (i.e., growth rates) suggested that chicks in a particular nest starved to death resulting in nest failure.

During 1995, we collected data on nest site characteristics for all 1994 and 1995 nests. For each nest, we recorded the species of tree in which the nest was placed, diameter at breast height (dbh) of the nest tree, height of

the nest, direction the nest faced relative to the center of the tree (unlike for nest cavity openings, determining this bearing for a nest cup was somewhat subjective and so we measured orientation to the nearest 45°; i.e., N, NE, E, SE, etc.), and distance to the nearest body of water. To characterize the habitat in the 10-m radius area surrounding each nest tree, we examined 12 variables in four quadrants (NE, NW, SE, and SW) around each tree. We measured distance to the nearest tree (dbh <10 cm) in each quadrant and recorded its dbh and species. Other types of woody vegetation fell into two categories: shrubs (multitemmed at base and height >1 m) and bushes (multitemmed but <1 m tall). For each quadrant we recorded the distance from the nest tree to the nearest shrub and nearest bush. For the purposes of data analyses, when there was no tree, shrub, or bush within 10 m, we entered this into the database as a missing value for distance. For each 10-m radius area, we estimated mean canopy height to the nearest 0.5 m in each quadrant using a Suunto optical reading clinometer, and we visually estimated the percent foliage cover to the nearest 5% for each canopy layer (tree, shrub, and bush), as well as for the extent of grass-forb ground cover and bare ground. We developed an index of overall vegetation density (value reflects percentage of sky blocked by vegetation) using a spherical densiometer held at elbow height in the middle of each quadrant. Except where noted, for statistical purposes we calculated mean values from the four quadrants for dbh of the nearest tree, distance to the nearest tree, distance to the nearest shrub, distance to the nearest bush, mean canopy height, percent canopy cover, percent shrub cover, percent bush cover, percent grass-forb ground cover, percent bare ground cover, and vegetation density. For nests found during 1996, we recorded data for orientation, height of the nest, and nest tree species, but no other vegetation variables due to logistical constraints.

We estimated solar insolation using the Arc Macro Language program Solarflux (Hetrick et al. 1993) for nest locations from 1995 and 1996 plotted on 1:50,000 scale topographic maps. Based on a 30-m horizontal resolution digital elevation model provided by R. Connell of the Toiyabe National Forest, we com-

pleted these calculations using the Arc/Info Grid Module. Variables estimated for each nest included total amount of solar radiation (kJ) incident on the nest tree's location for 1 May and 21 June, as well as the number of hours of direct sunlight expected with clear skies on those two days. These values incorporated the effects of topography around the nest, but did not account for the potential impact of local shading by adjacent vegetation.

Statistical analyses.—Because we did not collect data for all variables for each year of the study, sample sizes varied by analysis. To examine nest placement relative to the vegetation available in the immediate vicinity, we used paired *t*-tests to compare the dbh of the nest tree with the mean dbh of the nearest trees from all four quadrants. We also examined the choice of nest tree species at this localized scale by comparing the frequency of species chosen with the frequency of species detected as the nearest tree in the four quadrants for all nests. Using a *G*-test (Zar 1996), we evaluated choice after eliminating three species that had been used as nests but had not been identified among species of nearest tree in a quadrant for any nest. Those species eliminated included water birch (two nests), black cottonwood (*Populus balsamifera*; three nests) and willow (*Salix* spp.; eight nests).

The cover provided by nearby vegetation may have influenced nest placement through its effects on concealment of the nest and access to escape routes for attending adults (cf. Wiebe and Martin 1998). We used a two-tailed binomial test (Zar 1996) to assess the probability that the quadrant toward which the nest pointed had either the most dense vegetation (reflected through having the smallest distance to the near tree, the highest shrub cover, or the highest bush cover among the four quadrants), or the least dense vegetation (greatest distance to the near tree, the lowest shrub cover, or the lowest bush cover).

To test the hypothesis that robins changed the nest tree species they used over the season (Howell 1942, Savard and Falls 1981), we divided the nesting season into 15-day periods and compared the proportion of conifer nest trees (single-leaf pinyon or Utah juniper versus all other species) used from 1 May through 30 June using a *G*-test. We used a simple linear regression of nest height on

TABLE 1. Nest and local vegetation characteristics within 10 m of the nest for American Robins breeding in riparian habitat of central Nevada, 1994–1996.

Variable	Mean \pm SD	<i>n</i>
Nest height (m)	2.3 \pm 1.2	116
Nest tree dbh (cm)	18.5 \pm 9.0	62
Dbh of the nearest tree (cm) ^a	19.7 \pm 6.8	66
Distance to the nearest tree (m) ^a	6.3 \pm 2.3	70
Distance to the nearest shrub (m) ^a	4.6 \pm 2.8	70
Distance to the nearest bush (m) ^a	2.1 \pm 1.5	70
Height of the canopy (m) ^a	6.7 \pm 3.5	70
Percent canopy cover ^a	12.2 \pm 8.3	70
Percent shrub cover ^a	11.4 \pm 9.8	70
Percent bush cover ^a	11.4 \pm 8.6	70
Percent grass-forb ground cover ^a	27.1 \pm 15.2	70
Percent bare ground ^a	41.4 \pm 20.9	70
Vegetation density ^a	63.0 \pm 21.7	70
Distance to water (m)	19.3 \pm 17.3	70

^a Mean values for the four quadrants around the nest tree (missing values were ignored).

clutch initiation date to test the hypothesis of Howell (1942) that early breeding American Robins nested lower in trees than those nesting later.

Related to our examination of potential links between solar insolation or local vegetation and brood size at day 8, we analyzed orientation data using a Rayleigh test to determine the statistical significance of the mean angle for nests in each canyon (Zar 1996). For this analysis, we converted orientations (N, NE, E, . . .) to their 45° equivalents, analyzed the data, and then converted the resulting values back to the nearest orientation designation (N, NE, E, . . .) for presentation. Multivariate examination of vegetation characteristics versus clutch size, brood size at day 8, and brood loss included data from 1995 nests. We assessed the possible relationship between the solar insolation variables, nest orientation, estimated clutch initiation date, and our measures of productivity (clutch size, brood size at day 8, and partial brood loss which was represented as brood size/clutch size). We used a backward stepwise multiple regression to conduct the latter analysis. Similarly, we examined the association between local vegetation characteristics and our measures of productivity (clutch size, brood size at day 8, and brood loss) with the same technique. We used SAS version 8.12 (SAS Institute, Inc. 2001) for all statistical analyses; dependent variables were rank transformed for those data not normally distributed (Conover and Iman

1981). We considered relationships to be statistically significant when $P < 0.05$.

RESULTS

We found 132 American Robin nests in the five canyons, 42 from 1994, 28 in 1995, and 62 in 1996. The immediate vicinity around these nests was vegetated sparsely with trees, bushes, and shrubs, and there was limited cover at any canopy layer (Table 1). There were extensive amounts of bare ground around the nest trees and nests were substantial distances from the nearest water, given that most riparian strips were less than 50 m wide. Vegetation in the quadrant toward which the nest faced was neither the most nor least dense around the nest, based on distance to the nearest tree or percent cover by shrubs or bushes (P values for the six comparisons ranged from 0.13 to 0.76).

We found no significant difference between the dbh of nest trees and the mean dbh of the nearest trees in each of the four quadrants when all species were combined ($t = 0.83$, $df = 60$, $P = 0.41$; power = 100%). This pattern held also within species when we compared the dbh of aspen and pinyon nest trees with the mean dbh of the nearest conspecific trees around them (respectively, $t = 0.89$, $df = 18$, $P = 0.38$, power = 100%; $t = 0.79$, $df = 31$, $P = 0.44$; power = 100%; Table 2). Based on comparison with the percent availability of adjacent trees in the immediate vicinity of the nest (Table 2), American Robins used quaking

TABLE 2. American Robins breeding in riparian habitat of central Nevada, 1994–1996, used nest trees with a species composition significantly different from that available within 10 m of the nest tree (percentage reported with actual number in parentheses). Mean dbh for quaking aspen and single-leaf pinyon nest trees and the nearest adjacent conspecific were not significantly different.

Species	Used	Mean dbh \pm SD (<i>n</i>)	Available	Mean dbh \pm SD (<i>n</i>) ^a
Aspen	24.8 (31)	23.5 \pm 10.8 (18)	52.1 (110)	20.6 \pm 8.0 (18)
Birch	1.6 (2)		0	
Cottonwood	2.4 (3)		0	
Juniper	9.6 (12)		5.2 (11)	
Mountain Mahogany	5.6 (7)		3.3 (7)	
Pinyon	49.6 (62)	16.5 \pm 7.3 (31)	39.3 (83)	18.7 \pm 5.6 (31)
Willow	6.4 (8)		0	

^a Mean values for the conspecific nearest the nest tree within each of four quadrants around the nest tree.

aspen less frequently (24.8% of 125 nests) than expected and put their nests in single-leaf pinyon (49.6% of 125) more often than expected by chance ($G = 19.191$, $df = 3$, $P < 0.0001$). However, there was no significant change in the proportion of nests placed in conifers as the nesting season progressed from the beginning of May through the end of June ($G = 0.791$, $df = 3$, $P = 0.85$). We found a significantly positive relationship between nest height and clutch initiation date, but initiation date explained very little of the variance in nest height ($r^2 = 0.08$, $F_{1,69} = 5.77$, $P = 0.019$). Mean first egg date was 27 May (SD = 18 days, $n = 80$).

The mean angle of orientation for nests in each of the canyons indicated a tendency for the nest to face within the 90° arc between east and south (Table 3). However, only the data from San Juan Creek canyon, and all canyons combined, had a statistically significant vector. Although statistically significant in two cases, none of our incident solar insolation variables, nor orientation or clutch initiation date, explained biologically meaningful

amounts of the variation in clutch size ($r^2 = 0.06$, $F_{1,56} = 3.78$, $P = 0.06$; reduced model included only orientation), brood size at day 8 ($r^2 = 0.06$, $F_{1,76} = 4.43$, $P = 0.039$; reduced model included only solar insolation on 21 June), or partial brood loss ($r^2 = 0.08$, $F_{1,59} = 4.94$, $P = 0.030$; reduced model included only solar insolation on 21 June). Likewise, clutch initiation date was not significantly correlated with either solar insolation on 1 May or hours of direct sunlight on 1 May (Pearson correlation coefficients; $r = 0.18$, $n = 80$, $P = 0.11$, and $r = 0.16$, $n = 80$, $P = 0.13$, respectively).

We had insufficient data to examine the relationship of vegetation with clutch size or brood loss (data available on clutch size for only 14 nests from four canyons in 1995 when necessary vegetation data was collected). However, examination of the data on brood size at day 8 and vegetation variables indicated that mean dbh of the nearest trees, mean canopy cover, and mean canopy height were useful predictors, along with nest tree species, of brood size ($r^2 = 0.53$, $F_{6,16} = 3.05$, $P = 0.034$). Pearson correlation coefficients were negative for the three numerical variables, suggesting that brood size was higher where mean dbh of trees in the surrounding area was small, and both canopy height and canopy cover were low. Posthoc tests (PROC GLM; SAS Institute, Inc. 2001) for differences among nest tree types in day 8 brood sizes, however, were unable to distinguish the tree species involved for either this restricted database from 1995, or for a larger database of 80 nests from 1995 and 1996 for which we

TABLE 3. Orientation with respect to the tree trunk for the nests of American Robins breeding in the riparian habitat of five canyons in central Nevada, 1994–1996. There is a strong east to south tendency.

Canyon	Orientation	<i>n</i>	<i>Z</i>	<i>P</i>
San Juan	S	38	5.66	0.003
Clear	SE	33	2.38	0.093
Stewart	E	32	2.91	0.054
Washington	SE	6	0.25	0.829
Marysville	E	14	1.52	0.233
Combined	S	123	3.48	0.033

recorded both reproductive data and nest tree species.

DISCUSSION

The American Robin is an open country or edge species that often does well in suburban or modified rural habitats (Sallabanks and James 1999). Our results indicate that they also used relatively open habitat in desert-riparian communities. In qualitative comparison with the data presented by Sallabanks and James (1999) for robins breeding in Idaho, Washington, Oregon, and Montana, robins in our study population nested lower in trees and used trees with greater dbh. In addition, robins nesting in the Toiyabe Mountains of central Nevada occurred in forest stands with canopy covers that were lower than those of nest sites in the Pacific Northwest. Single-leaf pinyon and quaking aspen were the two most commonly chosen nest trees, but unlike the results reported by Howell (1942) for Ithaca, New York, and Savard and Falls (1981) for Toronto, Ontario, we found no seasonal shift in the tendency to use conifers, nor did we find as Howell (1942), despite a statistically significant relationship, a biologically meaningful association between the date of clutch initiation and nest height.

Contrary to the findings of Sallabanks and James (1999), American Robins in this population placed their nests at a particular orientation with respect to the center of the tree. Our study area was desert-riparian habitat, and the mean elevation for the 1995 and 1996 nests was $2,319 \text{ m} \pm 141 \text{ SD}$. Consequently, our observation of nest orientation from south to east suggests positioning to take advantage of early morning to midday heating after cool mountain nights, followed by shading in the afternoon during higher temperatures. This is consistent with arguments proposed for both New World (Balda and Bateman 1972) and Old World (MacLean 1976) desert-breeding species. Such thermoregulatory-based positioning also concurs with cavity orientation by Red-naped Sapsuckers (*Sphyrapicus nuchalis*) breeding in the same study area (Butcher et al. 2002). Previous studies of open cup-nesting species revealed a westward orientation for some (e.g., Hermit Thrush, *Catharus guttatus*, with a southward to westward tendency; Martin and Roper 1988) and others that were

less clear, with bimodal northward or southward orientations (e.g., Western Kingbirds, *Tyrannus verticalis*; Bergin 1991). However, although our nest orientation data suggests use of sites by American Robins with more exposure to the sun early in the day, we could not link this pattern to any of our measures of solar insolation. Likewise, there were no measurable associations among solar insolation, orientation, and clutch initiation date or brood size at day 8. Our analyses of tree density (as reflected in distance to the nearest tree) and vegetation cover at low to midcanopy levels (as reflected in percent shrub cover and percent bush cover) suggests that robins did not orient their nests in the tree toward either the most densely or sparsely vegetated quadrant immediately adjacent to the nest. This pattern was consistent with the finding of Wiebe and Martin (1998) that nest sites with intermediate levels of cover were sought out because they provided some concealment but allowed both the surroundings to be surveyed for predators, as well as a route for escape.

Productivity, as we measured it, appeared to be associated with the degree of openness of the canopy. The negative correlations among three variables related to the size and density of trees and brood size at day 8 indicates that robins nesting in open or edge habitat with a low and sparse canopy were more productive than were those nesting in areas with larger trees and greater canopy cover. However, variables related to the density or cover of either shrubs or bushes were absent from the regression. This result indicates that, at least for our study population, Davidson and Knight's (2001) hypothesis that edge effects related to shrub cover positively influence American Robin productivity is not supported. Results from studies of other species on the links between nest concealment and predation rates are contradictory and experimental studies suggest that nest concealment was not a factor in egg or nestling predation (Howlett and Stutchbury 1996). The absence of an association between brood size at day 8 and nest-concealing understory vegetation supports the idea that concealment, as we measured it, is a weak determinant of nesting success. Our results also differ from those of Hatchwell et al. (1996) in that we were able to identify features of the vegetation around the nest that

were useful in predicting the success during brood rearing, whereas Hatchwell et al. (1996) found such information useful only during the egg-laying and incubation periods.

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LITERATURE CITED

- ALDRICH, J. W. AND F. C. JAMES. 1991. Ecogeographic variation in the American Robin (*Turdus migratorius*). *Auk* 108:230–249.
- BALDA, R. P. AND G. C. BATEMAN. 1972. The breeding biology of the Piñon Jay. *Living Bird* 11:5–42.
- BERGIN, T. M. 1991. A comparison of goodness-of-fit tests for analysis of nest orientation in Western Kingbirds (*Tyrannus verticalis*). *Condor* 93:164–171.
- BUTCHER, L. R., S. A. FLEURY, AND J. M. REED. 2002. Orientation and vertical distribution of Red-naped Sapsucker (*Sphyrapicus nuchalis*) nest cavities. *West. N. Am. Nat.* 62:365–369.
- CONOVER, W. J. AND R. L. IMAN. 1981. Rank transformations as a bridge between parametric and non-parametric statistics. *Am. Stat.* 35:124–129.
- DAVIDSON, A. S. AND R. L. KNIGHT. 2001. Avian nest success and community composition in a western riparian forest. *J. Wildl. Manage.* 65:334–344.
- HATCHWELL, B. J., D. E. CHAMBERLAIN, AND C. E. PERINS. 1996. The reproductive success of Blackbirds *Turdus merula* in relation to habitat structure and choice of nest site. *Ibis* 138:256–262.
- HETRICK, W. A., P. M. RICH, F. J. BARNES, AND S. B. WEISS. 1993. GIS-based solar radiation flux models. *Am. Soc. Photogram. Remote Sens. Tech. Papers* 3:132–143.
- HOWELL, J. C. 1942. Notes on the nesting habits of the American Robin (*Turdus migratorius* L.). *Am. Midl. Nat.* 28:529–603.
- HOWLETT, J. S. AND B. J. STUTCHBURY. 1996. Nest concealment and predation in Hooded Warblers: experimental removal of nest cover. *Auk* 113:1–9.
- HUGHES, J. W. AND F. K. HUDSON. 1997. Songbird nest placement in Vermont Christmas tree plantations. *Can. Field-Nat.* 111:580–585.
- JUNG, R. E. 1992. Individual variation in fruit choice by American Robins (*Turdus migratorius*). *Auk* 109:98–111.
- KENEDEIGH, S. C. 1942. Analysis of losses in the nesting of birds. *J. Wildl. Manage.* 6:19–26.
- MACLEAN, G. L. 1976. Arid-zone ornithology in Africa and South America. Pp. 468–480 in *Proceedings of the XVI International Ornithological Congress* (H. J. Frith and J. H. Calaby, Eds.). Australian Academy of Sciences, Canberra, Australia.
- MARTIN, T. E. AND J. J. ROPER. 1988. Nest predation and nest site selection of a western population of Hermit Thrush. *Condor* 90:51–57.
- MARZLUFF, J. M. 1988. Do Pinyon Jays alter nest placement based on prior experience? *Anim. Behav.* 36:1–10.
- MÖLLER, A. P. 1988. Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. *Oikos* 53:215–221.
- PYLE, P. S., N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.
- SALLABANKS, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74:1326–1336.
- SALLABANKS, R. AND F. C. JAMES. 1999. American Robin (*Turdus migratorius*). No. 462 in *The birds of North America* (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.
- SAS INSTITUTE, INC. 2001. SAS statistical package, ver. 8.12. Sas Institute, Inc., Cary, North Carolina.
- SAVARD, J. P. L. AND J. B. FALLS. 1981. Influence of habitat structure on the nesting height of birds in urban areas. *Can. J. Zool.* 59:924–932.
- STAUFFER, D. F. AND L. B. BEST. 1986. Nest site characteristics of open-nesting birds in riparian habitats. *Wilson Bull.* 98:231–242.
- TYLER, W. M. 1949. *Turdus migratorius* Linnaeus: Eastern Robin. Pp. 14–45 in *Life histories of North American thrushes, kinglets, and their allies* (A. C. Bent, Ed.). U. S. Nat. Mus. Bull. 196:1–452.
- WEIXELMAN, D. A., D. C. ZAMUDIO, AND K. A. ZAMUDIO. 1996. Central Nevada riparian field guide. R4-Ecol-96-01. U.S. Forest Service Intermountain Region, Logan, Utah.
- WELTY, J. C. 1979. *The life of birds*. Saunders College Publishing, Philadelphia, Pennsylvania.
- WHEELWRIGHT, N. T. 1986. The diet of American Robins: an analysis of U.S. Biological Survey records. *Auk* 103:710–725.
- WIEBE, K. L. AND K. MARTIN. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Anim. Behav.* 56:1137–1144.
- YAHNER, R. H. 1982. Avian nest densities and nest site

selection in farmstead shelterbelts. *Wilson Bull.* 94:156–175.

YOUNG, H. 1955. Breeding behavior and nesting of the Eastern Robin. *Am. Midl. Nat.* 53:329–352.

ZAR, J. H. 1996. *Biostatistical analysis*, 3rd ed. Prentice Hall, Upper Saddle River, New Jersey.

APPENDIX

Ageing characteristics for American Robin chicks; Day 0 equals hatch day. Naming of feather tracts follows Welty (1979) except for the use of alula, primary, and secondary that follows Pyle et al. (1987). Development of feather sheaths was divided into four stages: (1) discoloration of feather tracts visible below skin, (2) feather sheaths visible under skin and causing skin surface to appear raised, (3) feather sheaths emerge from tract area but are not free of the skin, and (4) emergence of feather sheaths from the skin. Eyes were closed if they could not be opened by gently pulling the skin above them, partially open when nestlings could voluntarily hold eyelids open far enough for the eye to be visible, and open when the nestling could voluntarily hold its eyes open as adult birds do.

Age Diagnostic characteristics

Day 0 The capital region has two long tufts of down above the eyes and four tufts above the nape. The caudal tracts have tufts of down where each retrix will eventually emerge, the humeral area is covered with down, tufts of down are present where the secondaries will emerge, and the spinal area is covered by a single stripe of down.

Day 1 Light ridges appear on the skin of the breast and belly where the ventral feather tract discoloration will appear on day two.

Day 2 The capital, ventral, spinal, humeral, alula, primary, and secondary feather tracts become discolored. Discoloration appears as tiny gray to black dots. Discoloration of the secondary tracts is lighter than that of the primary tracts.

Day 3 Feather tract discoloration of the ventral, spinal, and humeral areas

changes from individual dots to solid areas of discoloration. Primary and secondary feather sheaths become visible under the skin as heavy ridges on the trailing edge of the wing. The first discoloration of caudal feather tracts appears.

Day 4 Nestling eyelids can be separated by gently stretching the skin above them upward. The alula feather sheaths become visible under the protuberance of skin on the leading edge of the wing. Primary and secondary feather sheaths extend from the trailing edge of the wing, but not from the skin, giving the trailing edge a serrated appearance.

Day 5 The nestling can hold its eyes partially open while handled. Feather sheaths become visible under the skin on the capital, ventral, spinal, and humeral regions. The alula feather sheath protrudes from the leading edge of the wing but is still covered by skin. Primary feather shafts emerge from the skin. Caudal tract feather sheaths become visible under the skin.

Day 6 Sheaths of the capital, ventral, spinal, humeral, alula, and secondary feathers emerge from the skin.

Day 7 The nestling can hold its eyes completely open and the caudal tract feather sheaths emerge from the skin.

Day 8 Day 8 nestlings are distinguishable from day 7 nestlings by the extent to which their feathers have broken from their sheath coverings. The ventral, humeral, and spinal areas are well feathered but the alula, caudal, and secondary feathers are still enclosed in their sheaths. Just the tips of the primary feathers are free from their sheaths. Nestlings also become very good at jumping, but still crouch down when returned to the nest, unlike their day 9 and day 10 siblings who try to leap out when returned.